A COMPARATIVE STUDY

OF THE CAROTID BODY AND CAROTID SINUS

OF VERTEBRATES

II

THE CAROTID BODY AND "CAROTID SINUS"

OF THE FOWL (GALLUS DOMESTICUS)

being

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by

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C O N T E N T S

INTRODUCTION

The findings discussed here are a sequel to previous work on the carotid body of submammalian forms and extends the study of the organ from the reptiles (Chowdhary 1950) to the birds.

A survey of the literature concerned with the carotid body and carotid sinus of birds reveals that very little work has been carried out on this subject.

Schaper (1892) in an extensive study of the carotid body of vertebrates was the first to investigate this organ in birds. He was unable to find any evidence of its presence, stating that "wenigstens trifft man in der umgebung der carotisbifurkation kein homologes organ" a view which no doubt arose from a failure to appreciate the development of the carotid system in birds.

Kose (1907) gives a detailed account of the carotid body in a number of different birds including the fowl. He makes use of four adult birds ranging in age from one to three years, and describes the carotid body as round or oval, situated near the cranial parathyroid and usually embedded in its hilum, the thick connective tissue capsule of the carotid body being in continuity with the connective tissue of the parathyroid/

parathyroid. He particularly stresses the thick nature of the capsule and its continuity with the parathyroid on the one hand and, through its artery of supply, with the adventitia of the carotid artery on the other. He describes the parenchyma of the carotid body as a compact mass of 'colourless chromaffin cells', which, though it would not take a yellow stain with chrome salts, he undoubtedly regards as chromaffin tissue. He also gives an account of the arterial supply of this structure.

Kose states that the carotid body is supplied exclusively by sympathetic nerve fibres, especially from 'a large ganglion nearby'. Terni (1931) traces the nerve supply of the carotid body of birds partly from the vagus and partly from the glossopharyngeal nerve, the latter through the precarotid nerve trunk. Muratori (1933 and 1934) studying the innervation in greater detail in a large number of different birds concludes, as a result of experimental work on fowl, that the carotid body is innervated almost exclusively by sensory fibres which have their cell bodies in the nodose ganglion of the vagus.

Watzka (1934), discussing the nature of the carotid body in vertebrates mentions that in the goose it is composed of non-chromaffin tissue and innervated entirely by the cranial parasympathetic.

The development of the carotid body of the fowl has also received only scanty attention. Verdun (1898) finds it arising from the mesoderm of the third arch artery. Szepsenwohl (1935) working on duck embryos comes to the conclusion that the carotid body separates off from the wall of the fourth aortic arch at the end of the sixth day, the cells composing it having migrated from the surface ectoderm to be incorporated in the arterial wall between the fifth and sixth day of incubation. Thus the carotid body of the duck would appear to be an ectodermal derivative, at least in part. Neither Verdun nor Szepsenwohl give any diagrams illustrating their findings. Dudley (1942) in dealing with the ultimobranchial body of the fowl illustrates some stages in the development of the carotid body.

Muratori (1934) makes a brief mention of the carotid sinus in birds, saying that the nerve supplying the carotid body also goes on to supply a portion of the wall of the carotid artery and suggests that this may represent the carotid sinus. Nonidez (1935) in a more detailed account describes a carotid depressor nerve. This is a branch from the nodose ganglion of the vagus which supplies the entire circumference of the common carotid artery at its bifurcation into the 'internal and external carotid' arteries. He regards this region as equivalent to the mammalian carotid sinus./

sinus. His material is limited to the study of six newly hatched chicks and he envisages the possibility of further anatomical changes in the carotid body with advancing age.

The present work is an attempt to clarify and extend these observations by studying the carotid body and carotid sinus of the fowl in greater detail, taking into account not only the gross anatomy and histology of these structures but also their blood supply, development and innervation.

MATERIAL AND METHODS

Twenty-three normal birds from six weeks to two and a half years of age were studied. At first the birds were killed with chloroform but coal gas was used subsequently for the great majority as it was found to give more satisfactory results. Because of variations in the histological picture obtained in the carotid body by using these two agents and in order to study the effects of other substances two additional birds were killed with potassium cyanide while anaesthetised with sodium nembutal.

The cervico-thoracic junctional region was exposed by splitting the sternum and the fixative was perfused through the ascending aorta. Several fixatives were used including Zenker-formol, Susa, formol-saline and Bouin. Bouin was found to be the fixative of choice for routine work as it not only gave the best fixation of the tissues but also had the additional advantage of permitting the use of most silver-on-the-slide staining methods. After about one hour a block containing the vagus, carotid artery, internal jugular vein, the two parathyroids, carotid body and the ultimo-branchial body was removed from each side and placed for a further 8 to 12 hours in the fixative, after which it was dehydrated in alcohol, cleared in benzene and embedded in paraffin./

paraffin. Except for three blocks which were cut longitudinally all the others were cut in the transverse plane. All sections were mounted serially. The following staining techniques were employed:-

Haematoxylin (Harris') and eosine	4 specimens
Iron alum haematoxylin and van Gieson's	6 "
Masson's acid fuchsin-ponceau-light green	2 "
Heidenhain's azan	2 "
Romanes' (1950) silver chloride	4 "
Ungewitter's (1951) urea-silver nitrate	3 "
Bodian's activated protargol	1 specimen
Cajal's silver pyridine	1 " .

An attempt was also made to demonstrate the vascular pattern of the carotid body by injecting filtered india ink into the carotid artery which was clamped above the origin of the artery to the carotid body. By this means four successful preparations were obtained.

Experimental procedures.

Eleven birds of both sexes, weighing between 425 grms. to 950 grms. were used for this study. They were anaesthetised with phenobarbitone sodium (Veterinary Nembutal, Abbott), the dose being calculated at 0.05 cc per 100 grms. body weight. This gave an entirely satisfactory anaesthesia lasting from half to one hour, the birds gradually recovering in three to eight hours. Larger birds weighing about

3000/

3000 grms. (2½ years old) responded very poorly to this and other anaesthetics, and were not used for experimental purposes.

All operations were performed on the left side leaving the right as a control.

In two birds the glossopharyngeal and vagus nerves were cut high in the neck and in a third only the glossopharyngeal was so treated. A curved incision was made along the lower border of the digastric muscle, the latter was retracted upwards and in the connective tissue subjacent to it the glossopharyngeal and vagus nerves were identified. The glossopharyngeal was traced upwards to its inferior ganglion and cut just below it, the vagus too was cut at this level.

In two birds the vagus nerve alone was cut in the middle of the neck. The nerve was exposed by a small longitudinal incision on the anterior aspect of the neck. The internal jugular vein which descends along the nerve was gently eased away from it and the nerve cut.

In the remaining six birds the left nodose ganglion was removed. An incision was made just to the left of the midline at the base of the neck and the vagus nerve together with the carotid artery and the internal jugular vein was/

was traced as it passed downwards towards the thorax between the cervical and clavicular air sacs. The nerve was gently eased from the surrounding tissues and traced downwards between the sir sacs to the nodose ganglion. The nerve was then cut just above and below the level of the ganglion which was removed. Since the ganglion is situated low down in the thoracic inlet some traction had to be applied to the vagus nerve in every case so as to obtain adequate exposure. The ganglion was not always very distinct but histological examination of the excised portion and the block of tissue removed at autopsy was used to confirm its removal.

All the birds were sacrificed on the sixteenth day after operation, fixed by perfusion with Bouin's fluid and blocks of tissue containing the carotid body were removed from both sides. The operated and control specimens from one bird in which the nodose ganglion was removed were stained by Masson's trichrome, the remainder being stained by the Ungewitter's urea-silver nitrate technique.

Development.

Two series of chick embryos were prepared in order to study the development of the carotid body. They were taken at daily stages from the third to the tenth day of incubation and thereafter every alternate day until hatching.

One/

One series was stained by haematoxylin and eosin while the other was treated for nerve fibres by the de Castro technique. Three embryos of the 7th, 8th and 9th day of incubation were stained by Bielschowsky's bulk silver-pyridine method, and some later embryos were also stained with Heidenhain's azan. All the embryos were cut serially in the transverse plane, though in the later stages only the lower cervical and upper thoracic regions were sectioned.

OBSERVATIONS

The carotid bodies of the fowl are situated in the thoracic inlet enclosed in the loose areolar tissue between the cervical and clavicular air sacs. The relations of the two carotid bodies, right and left, vary considerably though both lie lateral to the carotid artery and medial to the nodose ganglion of the vagus in a plane slightly ventral to these structures, the ganglion separating the carotid body from the internal jugular vein. The relation of the carotid body to the parathyroid glands shows considerable variation. In the 37 specimens studied it is found to be a close relation of the upper parathyroid in 5 cases (all left side), and of the lower parathyroid in 21 cases (12 right and 9 left), while in the remaining 9 (5 right and 4 left), it lies between the upper and lower parathyroid in a plane dorsal to both. In three out of 17 specimens taken from the right side the carotid body is found embedded in the hilum of the lower parathyroid gland. These findings are at variance with those of Kose (1907) who states, on the basis of 8 observations, that proximity to the lower parathyroid is the exception rather than the rule.

Caudally the relation of the carotid body to the ultimobranchial body is also variable on the two sides. On the/

the right side the lower pole of the carotid body invariably touches the ultimobranchial body, and may be completely embedded in it (3 cases), whereas on the left side the two structures are separated by a short interval, and in one case only it has been found in contact with the ultimobranchial body.

Except for those instances where the carotid body is embedded in the ultimobranchial body or in the parathyroids, it is seen as an independent organ connected to the surrounding structures only by its vessels and nerves.

Each carotid body is oval in shape and lies with its long axis inclined downwards and medially, the lower pole being nearer the carotid artery. In some instances (7 cases) the carotid body is seen to lie with its long axis more or less in the transverse plane partly curving round the carotid artery.

It is difficult to measure the size of the carotid body accurately because its fibrous capsule intermingles with the surrounding tissues and a large number of veins issue from it at different levels. However, in most cases it measures approximately 0.8mm. X 0.5mm. X 0.5mm., and is regularly present on both sides. Contrary to Kose's (1907) observations that this organ may be duplicated by the presence/

presence of a smaller body caudal to the main mass, it is always single.

Fig.1 shows the general position of the carotid body and its relation to the carotid artery, vagus nerve, and the lower parathyroid gland. The ultimobranchial body being low down in this specimen is not included in the reconstruction.

The blood supply of the carotid body comes directly from the carotid artery by a small branch which arises from the middle of the first part (the portion extending from the origin to the point at which it enters the prevertebral muscles in the midline) most usually in common with the artery to the ultimobranchial body and the inferior thyroid artery. The level of origin of the artery to the carotid body is fairly constant though its manner varies slightly in different specimens. Since no detailed account of the arteries of the base of the neck of the fowl is available the terminology used here is based on that given by Assenmacher (1953) in his description of the arteries of the neck of the duck which appear very similar in their arrangement.

The artery to the ultimobranchial body, the artery to the carotid body and the inferior thyroid artery most/

most usually arise by a common stem from the carotid artery (23/33 cases). This common stem has an extensive origin from the carotid but rapidly decreases in diameter before splitting into its three branches. In some instances the inferior thyroid artery arises approximately one millimetre higher than the remaining two which retain a common origin (7 cases). The artery to the carotid body has been found as a separate branch midway between the inferior thyroid artery above and the artery to the ultimobranchial body below in only three instances. Fig.2 shows the usual arrangement of these arteries in an injected preparation cleared in methyl salicylate.

Contrary to the observations of Nonidez (1935) the vertebral artery is seen to arise from the carotid artery at a much higher level and is not closely related to the carotid body in any way.

The capillary spaces within the carotid body are traceable in microscopic preparations directly into thin walled veins which pierce the fibrous capsule at many points. Though the artery of supply is always single and enters the carotid body at or near the lower pole the veins emerge from all parts of its surface, those issuing from the upper pole join to form three or four large tributaries which ascend for a/

a short distance and join the internal jugular vein either directly or indirectly through the veins draining the parathyroids. The remainder of the veins pass irregularly into those from the parathyroids and the ultimobranchial body.

The vagus nerve, as has been stated, passes lateral to the carotid artery and carotid body, and medial to the internal jugular vein. The nodose ganglion, a fusiform enlargement not always visible to the naked eye, extends from the level of the lower end of the thyroid gland above to the ultimobranchial body below. The carotid ramus of the nodose ganglion the 'ramo carotico del vago' of Muratori (1932) is seen to arise from the upper part of this ganglion and passes downwards to the carotid body along one of the many small veins draining the organ. On its way the nerve gives off small branches which enter into a plexus formation with adjacent nerve fibres which arise from the pre-carotid trunk and are apparently of sympathetic origin (Terni). In Fig.3 the carotid ramus is seen arising from the nodose ganglion but as it pursues a sinuous course it is seen cut at two places.

The prevertebral precarotid trunk of Terni which descends on the ventral aspect of the carotid artery, shows numerous small, irregularly placed ganglia one of which, containing/

containing large multipolar cells (Fig.4), is fairly constant in position. This will be referred to as the ganglion of the prevertebral precarotid trunk. It is nearly 0.1 mm. in diameter and lies near the origin of the artery to the carotid body, usually in the angle between the inferior thyroid artery and the carotid artery, at a slightly higher level than the carotid body. Fibres from this ganglion radiate in many directions and are distributed to the surrounding arteries as perivascular nerves. A very constant bundle passes laterally to join the carotid ramus of the vagus and is distributed with it. The direct passage of fibres from the prevertebral precarotid trunk of Terni into the nodose ganglion has been reported by Terni (1931) but is not seen in these preparations.

HISTOLOGY

The carotid body consists of a mass of epithelioid cells enclosed in a comparatively thick connective capsule which is a very prominent feature in sections, Fig.5. This capsule, which consists essentially of collagenous tissue with very few elastic fibres, is thickest at the superior pole where it may measure as much as 0.12 mm., but on the sides and at the lower pole it is thinner, varying from 0.04 to 0.08 mm. The fibrous tissue of the capsule is traceable to the adventitia of the blood vessels entering and leaving it as well as to the connective tissue sheaths of the nerves entering the carotid body.

The epithelioid cells lie within the capsule either as a single mass, or as is more common, in the form of two masses incompletely separated by a connective tissue septum derived from the capsule. Except for this the capsule does not send any major septa into the interior and in van Gieson and Masson stained preparations the epithelioid cells appear closely packed together without any intervening connective tissue stroma. At the extreme periphery of the cell mass fine collagenous strands can be seen to penetrate it for a short distance.

The cells are of two types (Fig.6). The majority of them are large epithelioid cells 8 to 10 μ in diameter/

diameter. They possess a large spherical, vesicular nucleus 6 to 8/u in diameter with a well-defined nucleolus from which a few strands of chromatin radiate towards the nuclear membrane. The cytoplasm of these cells stains a deeper colour with van Gieson or Masson stain and with the latter it appears finely granular. Intermingled with these are smaller spherical cells whose nuclei, 4 to 6/u in diameter, are frequently oval and have a darker, non-vesicular appearance owing to a more uniform distribution of chromatin material. The cytoplasm of these cells is non-granular.

The cellular differentiation is brought out clearly in silver stained preparations especially with the Ungewitter's and Bodian's techniques (Fig.7). The cell mass of the carotid body is composed almost entirely of large argyrophil cells usually with a single process gradually tapering to one side, but occasionally more than one process may be present. A large, vesicular nucleus, exactly similar to that in the epithelioid cells mentioned above, occupies the broad end of the cell and the cytoplasm contains much finely granular argyrophil material. The other cells show no argyrophilia and their cytoplasm is stained a uniform deep yellow in untoned preparations.

As will be described later, similar argyrophil cells/

cells are also found in the artery to the carotid body and in the wall of the carotid artery itself.

Both types of cells are freely intermixed and are disposed around narrow blood spaces. These latter are of the nature of thin-walled vessels with a lining of slightly swollen endothelial cells. Their connective tissue wall is just discernable at high magnifications as a thin blue line in Heidenhain's azan stain, but at places this appears to be absent altogether, only the endothelium then separating the epithelioid cells from the blood stream. In birds killed with chloroform these spaces are much less in evidence and the carotid body presents a more or less compact appearance, but in those killed with coal gas the spaces are clearly visible amd the rich vascularity of the organ becomes evident (Figs. 8 and 9). Also, in birds killed with potassium cyanide after nembutal anaesthesia, the picture is similar to that in the gas-killed preparations, the blood spaces being much in evidence.

The artery to the carotid body enters the organ somewhere in its lower half, often at the lower pole, passing obliquely upwards and outwards to emerge at the opposite side whence it is distributed to the lower parathyroid gland and the vagus nerve. Before entering the carotid/

carotid body the artery possesses a thick adventitial tunic which is continuous with the capsule of the carotid body. The media, though devoid of elastic fibres, is thick and composed of smooth muscle cells which have a swollen appearance with rounded rather than fusiform nuclei. Interspersed amongst the outer layers of these muscle cells are epithelioid cells of the same morphological features as are seen in the carotid body itself. These argyrophil cells are more commonly provided with blunt processes which very often penetrate among the smooth muscle cells, frequently reaching the intima. They have a certain resemblance to the dendritic cells found in the skin. The artery to the carotid body is richly innervated and the pattern is similar to the innervation of the carotid body.

The presence of argyrophil and non-argyrophil epithelioid cells in the wall of the artery to the carotid body, along with a dense plexus of interlacing nerve fibres, is a very characteristic feature and is present in every specimen, but is not seen in the other two arteries arising in common with it. In Fig.10, the artery to the carotid body and the artery to the ultimobranchial body can be seen arising from a common stem, but, whereas the former is heavily surrounded by these argyrophil cells the wall of the latter is quite devoid of them.

Within/

Within the carotid body itself the artery is not very easy to discern as throughout its course, skirting the cell masses, it gives off a large number of branches which immediately open into the spaces in the substance of the carotid body and the muscle cells of the media become directly continuous with the non-granular epithelioid cells (Fig. 5). Nevertheless, a more or less distinct channel with a thin muscular wall may be seen at places, especially at the periphery of the organ.

As the artery emerges from the carotid body the various coats gradually reappear. The carotid body is thus seen to lie in continuity with the wall of its artery of supply, the adventitia of which is continuous with the capsule and the media with the cellular elements of the medulla. This picture is similar to that of the carotid body of the dog described by Addison and Comroe (1942).

The innervation of the carotid body is by the carotid ramus of the nodose ganglion and by fibres from the precarotid trunk which it carries. The fibres enter the carotid body in groups of two or three in an irregular fashion at many points on the surface, usually in company with the veins (Fig.11). Once within the capsule they branch rapidly into a number of undulating filaments which interlace with other/

other similar branches producing a dense network of nerve fibres around the argyrophil cells. The fibres appear to be of two types, thick and thin, but a closer examination reveals that the same fibre in different parts of its course may appear as one or the other because marked variations in diameter occur within short distances. At places the fibres show localised varicosities where they may expand producing a neurofibrillar network (Fig.12). These expansions cannot strictly be called endings as the fibre can be traced in both directions away from them. When densely impregnated they appear as dark masses which, if situated near the capsule, frequently have connective tissue cells arranged more or less concentrically around them so as to give the impression of encapsulated nerve endings. Watzka (1934) using the bulk silver technique of Bielschowsky appears to have fallen into this error. With the silver-on-the-slide methods of Romanes and Ungewitter employed here the deposit of silver on the nerve fibres is much more delicate and precise and what appears to be an ending is clearly resolved into its components.

Nonidez (1935) has described two different types of nerve endings in the carotid body of chick. He considers, apparently without experimental proof of any kind, that the nerve endings of the vagal fibres are reticulated expansions while the endings of the glossopharyngeal nerve are fine terminals/

terminals ending in a ring form on or inside the cells. These reticular expansions are seen very clearly in the present specimens but seem to be subterminal in position as is frequently seen in other sensory endings. The nerve endings proper are more akin to the glossopharyngeal type of Nonidez though terminal rings and expansions which encircle the argyrophil cells have not been seen. Such endings are present both on the argyrophil and non-argyrophil cells inside the carotid body as well as on the cells around the artery supplying it. They seem to surround groups of three or four cells each rather than encircle each cell individually (Fig.13). In this respect they are similar to the nerve endings described by de Boissezon (1936) in the carotid body of horse.

The nerve supply of the carotid body of the fowl has been elucidated to some extent by differential section of the nerves which supply it. Section of the glossopharyngeal and vagus nerves above the level of the nodose ganglion has in all cases failed to produce any significant difference in the pattern of innervation while removal of the nodose ganglion itself has in all cases reduced the number of nerve fibres markedly (Fig.14). In the latter instances whereas the carotid ramus of the nodose ganglion is completely degenerated/

degenerated, the bundle coming to join it from the ganglion of the precarotid trunk also shows some loss of fibres, though this is never complete. The persisting fibres in this bundle are traceable to the cells in the ganglion. In the carotid body itself there is almost complete degeneration of the fibres supplying the cellular mass. A few thin fibres which persist, come from the precarotid trunk, are seen related to the blood vessels and reach the wall of the carotid artery along the artery to the carotid body. It is possible that the traction necessary to expose and remove the nodose ganglion may have damaged these fibres coming from the precarotid trunk. Though the nerves in the carotid body are almost completely degenerated after removal of the nodose ganglion the morphology of the cellular components is quite unaffected, in fact, in one such bird where the preparation had been stained with Masson's trichrome no difference could be seen between the operated and the control sides. It could be that the period of 16 days allowed after the operations is not long enough to affect the cellular elements which might have undergone some atrophy if the birds had been allowed to survive for a longer period.

To sum up, the innervation of the cell mass of the carotid body is derived exclusively from the vagus while the precarotid trunk, being a sympathetic trunk (Terni 1931) appears/

appears to supply only perivascular sympathetics to the blood vessels of the organ.

One other interesting fact regarding innervation may be mentioned here. A glomus body is found very frequently in relation to the carotid ramus of the vagus. It is a rounded collection of epithelioid cells enclosing capillary spaces to and from which an artery and a vein can be traced. The cells are non-argyrophil thus differing from those in the carotid body. Fibres of the carotid ramus surround the glomus body on their way to the carotid body. De Boissezon (1944) has described and illustrated 'intra neural paraganglia' in the course of the nerves to the carotid body of the horse which appear to be very similar.

A careful search for other paraganglionic masses elsewhere in the neighbourhood of the carotid body reveals no such structures. Although groups of 4 to 6 cells of an epithelioid type are visible scattered throughout the nodose ganglion of the vagus, closer examination reveals that these are capsular cells which have been cut tangentially since adjacent sections show the body of the cell which they surround. Nothing comparable to the paraganglionic masses described by Muratori (1932) in the canary and sparrow has been found in the fowl.

The/

The region of origin of the artery to the carotid body.

It is necessary to describe this portion of the carotid artery under a separate head because of its structural differences from the rest of the arterial wall. Both Muratori (1934) and Nonidez (1935) regard it as corresponding to the mammalian carotid sinus due mainly to its richer nerve supply.

This region extends for approximately 1.0mm. to 1.5mm. confined to the lateral wall of the carotid artery just above the origin of the artery to the carotid body, irrespective of the mode of origin of the latter. The adventitia of the carotid artery, usually 0.003 to 0.004mm., is thickened to as much as 0.015mm. in this region, and in the media, which is not thinner than elsewhere, there are collections of cells which appear different from the surrounding smooth muscle. They are composed of large epithelioid cells and are arranged in radially disposed triangular shaped groups whose base frequently extends to the intima while the apex passes towards the adventitia, thus interrupting the elastic laminae in the media of the carotid artery (Fig. 15). Histologically the cells are similar to those in the carotid body or in the wall of the artery to it, and in silver preparations the argyrophil and non-argyrophil types are again visible (Fig. 16). The blood supply of these cell/

cell masses is derived from a slender branch which arises from the artery to the carotid body just as it enters the lower pole of this organ. This artery passes through the carotid body and crosses over to enter the adventitia of the carotid artery where it breaks up to supply these cells. Curiously enough, both inside the carotid body and in the wall of the carotid artery this vessel has remarkably thin walls which are quite well-formed in the intervening portion. A few thin-walled veins, evidently draining these cell masses are present in the adventitia and join the veins issuing from the carotid body to drain into the parathyroid venous plexus. Thick nerve fibres from the carotid body are traceable along the veins to these cell masses in the carotid wall where they end by winding round groups of three or four cells each in a fashion exactly similar to that in the carotid body (Fig. 16). In the birds in which the nodose ganglion was removed these nerves degenerate completely except for an occasional fibre here and there, but, as in the carotid body, the epithelioid cells show no histological changes (Fig. 17).

The close relation of the vascularity of this region to that of the carotid body as well as the presence of a common innervation of both are significant facts, still, it is not possible on histological evidence alone to label this region/

region as a carotid sinus. In mammals the thinning of the media and the presence of specialised nerve endings (reticulated, disc-like or miniscal) limited to the adventitia are characteristic features (de Castro 1928), but in the fowl the media is uniformly thick throughout and the nerve fibres terminate as free nerve endings winding round groups of epithelioid cells which lie within the media and are not characteristic constituents of the mammalian carotid sinus.

The epithelioid cells of the carotid body in addition to forming the main mass of the organ are evidently continued also as a cuff around its artery of supply as well as over a small area of the wall of the carotid artery where they are present as isolated collections of cells. Their pattern of innervation is similar in all cases and is derived from the vagus.

DEVELOPMENT

The earliest manifestation of the carotid body is in 6-day embryos in the form of a plaque-like thickening of the lateral wall of the third aortic arch near its mid-point. Careful examinations of earlier embryos have failed to reveal the presence of this organ in any form. Szepsenwohl (1935) describing a migration of cells from the surface ectoderm into the wall of the fourth arch artery states that these later separate off as the anlage of the carotid body. In the present series of embryos no evidence has been found of any such direct migration of ectodermal cells into the carotid body anlage and it is quite certain that the fourth arch artery is not concerned in the formation of this structure.

In the 6-day embryo the margins of the carotid body anlage are not sharply defined because the superior parathyroid is partially fused with it, but by the 7th day it becomes more clearly defined as it separates from the parathyroid (Figs. 18 and 19). At this stage it is seen as a thickening of the lateral wall of the third arch artery situated midway between the origins of the secondary subclavian and vertebral arteries. The superior parathyroid is lateral/

lateral to it but separated by a little loose mesenchyme, while the nodose ganglion is posterolateral. The ultimo-branchial body lies caudally and in a more medial plane with the third arch artery intervening between the two.

Subsequently with the elongation of the neck and the caudal shift of the heart, the third arch, or the carotid artery as it may now be called, assumes a more vertical position. The carotid body anlage increases in size and gradually gets detached from the arterial wall except for its connection through its artery of supply. It continues to lie lateral to the artery but passes into the angle between the nodose ganglion and the parathyroid. By this time, the superior parathyroid has shifted cranially and the carotid body now lies in relation to the inferior parathyroid, a position which it retains in the majority of cases. The ultimo-branchial body also comes in contact with the lower pole of the carotid body by the 9th or 10th day and remains so till the 14th day after which the two organs again separate from one another, except in a few cases.

At first the anlage of the carotid body is not distinguishable histologically from the wall of the carotid artery. Both consist of fusiform, closely packed cells, with/

with oval nuclei and non-granular faintly eosinophilic cytoplasm. By the 8th day the cells are still fusiform but they are more loosely arranged around small blood spaces which are continuous with the lumen of the carotid artery and contain an occasional blood cell. By the 9th day the cells, particularly those near the centre of the carotid body, begin to lose their elongated shape and become more spheroidal, though the nuclei are still similar in appearance and the cytoplasm remains agranular. The carotid artery sends in a small branch (Fig. 20) which is distributed to this mass and continues through it upwards to the parathyroids. This early vascularisation of the condensation is a very interesting feature.

There is no material change in the appearance of the cells of the condensation till the 14th day, the cells differing from those in the arterial wall only in their shape, but from the 14th day onwards there is a rapid change in appearance and the true epithelioid cells become apparent. The cells completely lose their elongated shape and become spheroidal with the characteristic vesicular nucleus and faintly granular cytoplasm (Fig. 21). The cells with more compact nuclei and nongranular cytoplasm also appear in great numbers. The earliest appearance of argyrophilia in these cells cannot be established with certainty because of the unreliable/

unreliable results obtained with Ungewitter's technique in embryonic material and with the bulk silver stains the argyrophilic nature of these cells is not demonstrated at any time. It is probable, however, that the process starts somewhere between the 16th and 18th day, because in two successful Ungewitter's preparations the argyrophil cells are absent at 16 days but present in considerable numbers in the 18-day embryo (Fig. 22).

An important feature in embryos of 7 to 11-days is the presence of numerous small, rounded, deeply chromatic cells aggregated in an irregular mass in the gap between the vagus, parathyroid and the carotid artery (Fig. 23). These cells are first seen at the 7-day stage migrating from the vagus and are joined later on the 8th day by similar contributions from the precarotid trunk and the recurrent laryngeal nerve. In all cases they are seen clustered around the developing carotid body but never seem to enter it, some strands even pass round the carotid body to reach the carotid artery at the site of origin of the artery to the carotid body, but, again, they remain detached from the wall of the carotid artery and appear to take no part in its development. After the 11th day their number gradually diminishes and by the 16th day only a few are seen scattered here/

here and there. It is difficult to say whether they do or do not contribute any specific elements to the carotid body itself. They are highly suggestive of Schwann cells preceding the nerve fibres themselves and would seem to correspond to the cells which Boyd (1937) considers to be 'preneuroblasts'.

The capsule of the carotid body at the 14th day is poorly developed consisting of a slight condensation in the loose mesenchyme which surrounds it. Subsequently it gradually increases in thickness and density till in newly hatched chicks it forms a well-developed covering.

The nerve supply of the carotid body can be traced even in the earliest stages from the nodose ganglion of the vagus. The precarotid trunk of Terni and the recurrent laryngeal nerve by their intercommunication with each other and with the branch from the vagus form a complicated plexus. In the 7-day embryo a small branch is seen to arise from the nodose ganglion and pass towards the anlage of the carotid body which at this stage shows no nerve fibres within it. By the 8th day this carotid ramus of the vagus becomes more distinct and communicates with a plexus in front of the carotid artery surrounding the commencement of the inferior thyroid artery. This plexus is formed of fibres of the precarotid trunk intermingled with those from the vagus and the/

the recurrent laryngeal nerve (Fig. 24). A group of nerve cells is also found in its midst and is the lowest of the irregular groups of small cells disposed along the ventral side of the carotid artery. The precarotid trunk reaches this point mainly by continuing its downward course along the carotid artery, but also by way of a branch which passes through a group of nerve cells at the origin of the vertebral artery. This branch can be seen as early as the sixth day (Fig. 25) passing lateral to the carotid artery and between it and the nodose ganglion. It may be so intimately related to the vagus as to appear to be blended with it, but by careful examination it can always be traced forwards as a distinct bundle joining the ganglionic mass of the main precarotid trunk lower down. In Fig. 26 this bundle is seen crossing the carotid artery on its lateral side to join the ganglion of the precarotid trunk.

In the later stages of development the carotid ramus becomes more prominent and from the communication between it and the ganglion of the precarotid trunk a nerve bundle is seen to pass caudally at the 10-day stage. It has now approached the adult pattern of innervation where the carotid ramus and the branch from the precarotid trunk form a loop from which the carotid body is supplied.

It is interesting to note that whereas in mammals there is considerable migration of nerve cells along the nerves into the carotid body, the carotid ramus of the vagus in the chick shows only three or four scattered nerve cells along its course and there is no migration of nerve cells from the ganglion of the precarotid trunk. From the 10th day onwards one can see a thick nerve trunk arising from the vagus, at the level of the lower pole of the carotid body, and carrying a large number of nerve cells along its course. This is the accessory depressor nerve of Monidez (1935) and though some of its fibres are traceable into the carotid body the neuroblasts remain separate. Although the main nerves supplying the carotid body are established by the 10th day there are very few fibres within the organ at this stage (Fig. 27), but their number slowly increases and in 12-day specimens they are traceable through the carotid body to pass to the wall of the carotid artery, where they form a comparatively rich plexus of nerves (Fig. 28). From the 14th day onwards, while the mesodermal cells are changing into epithelioid cells, the carotid body shows a dense innervation almost approaching the adult picture in de Castro's preparations (Fig. 29). A well-developed nerve plexus is also present in the wall of the carotid artery by this time.

As has been mentioned already the exact period of development of argyrophilia in the epithelioid cells has not been determined though in the 18-day specimen a number of argyrophil cells are seen inside the carotid body for the first time. In the wall of the carotid artery, however, argyrophil cells are as yet absent, though they are present in the wall of the artery to the carotid body (Fig. 22). In the newly hatched chick the process of differentiation of these cells has spread to the wall of the carotid artery so that by this stage the adult arrangement has been achieved.

Thus the appearance of nerves within the carotid body precedes the maturation of the epithelioid cells and is in advance of similar processes in the wall of the artery to the carotid body and the carotid artery itself. It may be that the development of the argyrophilia in the epithelioid cells, extending from the carotid body along its artery of supply to the carotid artery is dependent on their innervation by the vagus, but certainly short term denervation is not associated with a loss of argyrophilia.

The development of the carotid body, therefore, starts first as a mesodermal condensation from the wall of the third arch artery between the sixth and seventh day, separating from the artery between the 8th and 9th day, but innervation/

innervation by fibres from the nodose ganglion of the vagus and the precarotid trunk increases slowly from the 10th day onwards, becoming more rapid after the 14th day so that by the 18th day it has acquired all the adult histological features. Contrary to the development in mammals, very few neuroblasts are found migrating into the mesodermal anlage. The epithelioid cells seem to be derived entirely from the mesodermal constituents of the wall of the third arch artery and no evidence of any significant contribution of ectodermal origin has been found.

DISCUSSION

Schaper's (1892) observation that the carotid body is absent in birds is not surprising in view of the fact that the embryology of the aortic arches of the chick was insufficiently understood at that time and a search at the definitive bifurcation of the carotid artery would show no such organ. On the other hand, Nonidez's (1935) emphatic contention that the carotid body of chick is located at the bifurcation of the common carotid into its internal and external branches is more difficult to understand. Regardless of embryological data he interprets the site of origin of the vertebral artery as the bifurcation of the common carotid because, according to him, the carotid body is situated near it and the nodose ganglion of the vagus is at this level 'exactly as it happens in the mammal', this despite the fact that it is uncommon for the mammalian nodose ganglion to lie at the level of the bifurcation of the carotid artery, usually it is situated at a higher level.

Both Twining (1906) and Hughes (1934) have made it clear that the definitive external carotid artery is a secondary formation from the dorsal aorta, and the ventral aorta in front of the third arch atrophies by the sixth day. In the adult, therefore, though the carotid body is invariably related/

related to the carotid artery and obtains its blood supply from it, it is quite distinctly separated from the vertebral artery and it is never seen in relation to the 'embryonic' carotid bifurcation, since the carotid body appears in the middle of the third aortic arch well separated from the ventral end of the second arch at a time when the latter is already disappearing.

Kose (1907) has given an exhaustive account of the gross and microscopic anatomy of the carotid body of fowl, but his material, limited to four adult birds, cannot admit of generalisations. As a rule, the carotid body is related to the inferior parathyroid gland and only in exceptional cases it may be located at a higher level, medial to the superior parathyroid. Since in the majority of the specimens the carotid body is found free from the surrounding structures, Kose's emphasis on its proximity to the parathyroid seems hardly justifiable. In this limited space occupied by the thyroid, thymus, parathyroids, ultimobranchial body and the carotid body, the location of the latter beside the parathyroid is apparently incidental.

According to Kohn's (1900) classification the carotid body of the fowl belongs to the compact type and its structure does not present any marked differences from that of mammals/

mammals. As in the latter, it consists essentially of a mass of epithelioid cells surrounding capillary blood spaces of a sinusoidal type. Two types of cells are distinguished in the cell mass. A large epithelioid cell with one or more processes projecting from it, a vesicular nucleus and granular, argyrophilic cytoplasm. These cells, which may be called the type I cells, constitute by far the largest numbers and are seen not only in the carotid body itself but also in the walls of the artery supplying it and in a circumscribed region of the wall of the carotid artery adjacent to the origin of the artery to the carotid body. The other cells, type II, are also epithelioid in appearance though smaller in size. They have a denser nucleus and nongranular cytoplasm and are seen here and there, singly or in groups, amidst the type I cells. By following the artery to the carotid body into the organ it can be seen that the smooth muscle cells of the media gradually assume a spheroidal shape and become continuous with the type II cells.

Two types of cells have also been described in the mammalian carotid body, but there seems to be considerable difference of opinion concerning them. Paunz (1923) recognises large epithelioid cells with vesicular nuclei which constitute the main mass of the carotid body while other smaller cells with pyknotic nuclei are regarded by him as degenerative/

degenerative forms of the first type resulting from post-mortem changes, a view supported by Gosses (1937).
White (1935) regards the two cells as independent of one another. He stresses the fact that there are only two types of cells in the carotid body parenchyma, with no transitional stages between them and that "sie (the two types of cells) zwei ganz verschiedene Typen darstellen und wahrscheinlich von verschiedener Herkunft und Funktion sind". According to him there are cells with compact pyknotic nuclei which appear very much like plasma cells and may form a syncytium with neighbouring cells of a similar type. The other type, which he does not seem to lay much stress on, have large, oval, vesicular nuclei poor in chromatin. He is uncertain which of these cells constitute the specific elements of the carotid body, but has illustrated his work with some excellent photomicrographs from which it is evident that his second type of cell corresponds to the type I cell of this work and forms a greater part of the carotid body than the smaller cells corresponding to type II described here. In his specimen of the carotid body of pigeon he does not mention whether he finds these two types of cells or not, but he states that they form a protoplasmic syncytium. Unfortunately his photomicrographs of the carotid body of pigeon are not sufficiently clear to allow any conclusions to be drawn.

In/

In the carotid body of horse Meijling (1938) recognises that the chief cells have large vacuolated nuclei. He compares them in their staining reactions with nerve cells and regards them as modified neurones. However, he also mentions protoplasmic strands with deeper staining, oval, or rounded nuclei penetrating between the chief cells and which, he presemes, are syncytial strands derived from the capsule.

Recently, de Kock (1951), using Holmes' silver technique has demonstrated two types of cells in the carotid body of cat. The main cells are large with vesicular nuclei and 'very granular cytoplasm'(type I) while smaller cells with more compact nuclei and agranular, pinkish-red cytoplasm (type II) are also present. She does not mention any argyrophilia in either, still it is quite probable that they are the same two types as are seen here in the fowl.

The majority of the authors (Schaper 1892, Paunz 1923, Meijling 1938, Hollinshead 1943, etc.) seem to agree that the specific cells of the carotid body are those which are here called type I, and which in this study are typically argyrophilic. It is more difficult to say whether the type II cells are a different form of specific cell of the carotid body or merely modified stroma cells derived from the coats of the artery, whether from the media, as appears to be the case here, or from the connective tissue capsule as Meijling (1938) believes. That they are not the result of post/

post-mortem degenerative changes is clear from the fact that they are seen constantly in the carotid body of fowls fixed by perfusion within a few minutes of death.

The blood supply of the carotid body of the fowl is derived exclusively from the carotid artery, either independently or in common with the inferior thyroid artery and/or the artery to the ultimobranchial artery. The wall of the artery to the carotid body has few elastic fibres and lacks an internal elastic lamina, while the smooth muscle cells gradually merge into the epithelioid cells type II of the carotid body. Interspersed amongst these are strongly argyrophilic type I cells which, in this region, show more processes than in the carotid body. These processes penetrate towards the lumen of the artery between the muscle cells. Except for these argyrophil cells the other features of the artery to the carotid body have been observed also in the artery of supply of the mammalian carotid body (de Boissezon 1943, Addison and Comroe 1942). The artery to the carotid body as it skirts the organ, running between the cell mass and its capsule, penetrates the latter at the opposite side and passes to supply the nodose ganglion of the vagus and the parathyroids. In its passage through the carotid body it opens out directly into the blood spaces without the intervention of arterioles, an important point in favour of its being a modified form of arteriovenous anastomosis.

The/

The presence of argyrophil epithelioid cells in the wall of the artery to the carotid body and of identical cell groups in the adjoining regions of the carotid artery, combined with the absence of such structures on adjacent vessels is highly suggestive that the process of migration outwards of the carotid body elements is incomplete in the fowl. In the lizard, in the vicinity of the origin of the internal carotid artery, Adams (1953) has described small aggregations of specialised epithelioid cells invariably present in thickenings of the adventitia which are well supplied with vessels. He believes that they correspond to the mammalian and avian carotid body. In the fowl, the carotid body elements appear to have progressed a stage further in their separation from the carotid artery and while forming a well-defined mass, they share their vascularity and nerve supply with similar elements still incorporated in the wall of the carotid artery. It is of interest that this region of the carotid artery lacks the definite characters of the mammalian carotid sinus since there is no thinning of the media and no special nerve endings are present. Apart from its profuse nerve supply there is no anatomical evidence that this region is homologous with the carotid sinus of mammals, and, though physiological experiment alone can clarify this point, it would be of interest if the same tissue elements act as chaemoreceptors at one place and as baroreceptors at another.

Terni/

Terni (1931) describes the innervation of the carotid body from the precarotid trunk as well as by fibres from the vagus and the recurrent laryngeal nerve, though he does not stress the relative importance of each. Basing his observations on embryos at different stages of development he describes the precarotid trunk as a sympathetic strand formed by a longitudinal splitting of the primitive sympathetic cord. This is joined later by a twig from the glossopharyngeal nerve at the base of the skull, and lower down in the neck fibres are distributed from it to the carotid body. Thus he regards the precarotid trunk as the homologue of the intercarotid nerve of mammals. Muratori (1932 and 1934) on much more conclusive evidence has established that the fibres supplying the carotid body of birds come from the nodose ganglion of the vagus and this has been confirmed in the present work. The few fibres which persist after extirpation of the nodose ganglion are always traceable to the multipolar cells of the ganglion of the precarotid trunk. The possibility that some glossopharyngeal fibres might reach the carotid body via the communication between the vagus and the glossopharyngeal nerves high up in the neck (anastomosis of Staderini) is ruled out by the fact that no degeneration of the fibres within the carotid body can be shown when the vagus nerve is cut above the level of the nodose ganglion.

The nerve endings in the present specimens are slightly different from those reported by Nonidez (1935) in the carotid body of newly hatched chicks. Reticulated expansions, where the nerve fibres seem to expand into a neurofibrillar network, are seen only on the course of the nerve fibres and the endings themselves are simple fine nerve terminals which wind round groups of three or four cells each. The pictures obtained by Romanes' silver chloride, Bodian's activated protargol, and Ungewitter's urea-silver nitrate techniques are all alike and it is hardly possible that staining technique may be responsible for this difference.

With regard to the innervation of the two types of cells in the carotid body, De Kock (1951) has traced a rich plexus of nerves which supplies the type I cells and also passes to innervate the type II cells. In the present study no more can be said than that both types of cells are richly innervated and that the nerve fibres passing to them have a common origin in the nodose ganglion of the vagus, a fact demonstrated by the equal loss of nerve fibres to both groups of cells when the ganglion is removed, though no such loss is observed when the vagus is cut at a higher level.

Paraganglionic masses, described by Muratori in the sparrow, have not been seen in any specimen and it seems doubtful/

doubtful if this is attributable simply to a species difference.

The development of the carotid body in the fowl is, with minor exceptions, similar to that in mammals. It commences as a thickening of the lateral wall of the third arch artery and appears to be composed entirely of mesodermal cells. According to Verdun (Kose 1902) it first appears on the ninth day but is visible much earlier than this, for though it is definitely seen on the 7th day it can be made out with a little difficulty even on the sixth day. It is interesting to note that the ductus caroticus of the chick atrophies at about this time and it is perhaps more than incidental that the carotid body anlage should appear just at this stage, for even in human embryos its appearance is associated with similar changes in the vascular tree (Boyd 1937).

From the very beginning the condensation is on the lateral wall of the third arch artery, while in mammals it has been noted as occupying the whole circumference of the artery at first, though later it is confined to the lateral side (Boyd 1937, Hammar 1934). In subsequent development the early vascularisation is an interesting feature while innervation is a comparatively late event. Though it is evident/

evident that the carotid body of the chick is essentially a mesodermal derivative, it has to be appreciated that the final histological picture is not attained till shortly before hatching at a stage when innervation is complete. The innervation of each region precedes the appearance of argyrophil cells by approximately eight days, nerve fibres reaching the carotid body and its artery of supply first, prior to the innervation of the wall of the carotid artery. This suggests that either the argyrophil cells are mesodermal elements which may differentiate under the influence of the ingrowing nerve fibres or that they enter the innervated regions together with the nerves and subsequently develop their adult characteristics. The ectodermal origin of the cells has to be considered, several authors having described such contributions from many sources, notably from the ectoderm of the third arch (de Winiwarter 1939), the ectoderm of the fourth arch (Szepsenwohl 1935), in the form of 'preneuroblasts' as Boyd (1937) mentions for the human carotid body, or as 'embryonic sympathetic cells' from the surrounding nerves (Smith 1924). de Winiwarter has described the migration of ectodermal cells into the early mesodermal anlage of the carotid body in pig embryos, but careful search for a similar migration of cells in the carotid body of the chick has yielded negative results. In the 3-day embryo the epibranchial/

epibranchial placode of the third arch loses its basement membrane and sends inwards masses of cells which form the petrosal ganglion of the glossopharyngeal nerve. These cells, which are indistinguishable from the surrounding mesoderm except for their slightly denser stain, lie beside the artery of this arch which, at this stage, has only a thin endothelial lining as a wall. No migration from these placodal cells can be seen at this or subsequent stages, and it seems unlikely that any placodal elements become invisibly incorporated in the wall of the artery though it may be that this contact in some way 'induces' the arterial wall to form the carotid body anlage.

The nature of the carotid body of birds has been discussed only by Kose (1907) and Watzka (1934). The former regards the carotid body as a paraganglion composed of colourless chromaffin cells "farblose chromaffinenzellen", and Watzka, subscribing to this view explains the failure of these cells to stain with chrome salts on the grounds that they are paraganglia of the parasympathetic system and thus do not show the same staining reactions as the paraganglia of the sympathetic system. The word 'paraganglion' has been employed so loosely in the literature that it is difficult to determine exactly what is meant by it, different workers having used the term to signify different things. In any case, it implies at least a tissue/

tissue derived from the nervous system (Kohn 1903) and this cannot be said with absolute certainty about the carotid body of the fowl. Apart from the possible exception of Schwann type cells neural elements are not traceable into the carotid body of the fowl at any stage of development.

Schumacher (1938) believes the carotid body to be an arteriovenous anastomosis and compares it to the coccygeal body, the epithelioid cells of the carotid body being, according to him, modified smooth muscle cells of the wall of the artery of supply. If this was the case it would imply that the carotid body is of mesodermal origin.

On the other hand Hollinshead (1941), after carefully studying the structure of the carotid body and the coccygeal body, concludes that the two are of an entirely different nature, because the coccygeal body lacks the dense innervation of the former and the staining reactions of the carotid body are quite different.

Goormaghtigh and Pannier (1939) take an intermediate stand and conclude, from studies on the supra-cardiac body of the cat, that the carotid body represents an arteriovenous anastomosis associated with a paraganglion, secretions from which in some way affect the functioning of the/

the vessels in it. They even describe a rudimentary axis-cylinder from the paraganglionic cells. While this view has much to be said both for and against it, the illustrations of their work showing the supracardiac bodies of the cat in no way resemble the carotid body in mammals or birds. Whereas Kohn (1900), Kose (1907), Watzka (1934), Meijling (1938) and Hollinshead (1943) have all attempted to interpret the carotid body in terms of a single specific cell, Goormaghtigh and Pannier are probably the first to appreciate the presence of multiple elements combined in a composite organ, a view which appears quite plausible considering the structure of the carotid body in the fowl. There is little doubt that the blood spaces within the organ are placed directly between the artery of supply on the one hand and the collecting veins on the other. The vascularity of the carotid body varies at different times as can be seen by comparing Fig. 8 with Fig. 9. The first shows the carotid body as a compact mass of cells with narrow indistinct blood spaces but the blood vessels in Fig. 9 are wide open and the carotid body appears as masses of epithelioid cells separated by capillary spaces. To appreciate how the vascularity of this organ varies from one specimen to another one has only to compare the illustrations of Schaper (1892), Gosses (1937) and Meijling (1938) who show a highly vascular carotid body, with those of/

of Riegele (1928), Muratori (1934), Nonidez (1935) and Hewar (1948) where the carotid body appears as a solid mass with few vessels in it. This variation of the vascular pattern is in keeping with the interpretation of the carotid body as an arteriovenous anastomosis, as is the continuity of the muscle tissue of its artery with the type II cells, the major difference being the presence of the type I argyrophil cells.

It is these argyrophil cells which most workers, excluding White (1935), have considered as the chaemoreceptor elements, and Goormaghtigh and Pannier have interpreted as the paraganglionic cells, the blunt processes of which they describe as rudimentary axons, while others consider them as modified neurones (Meijling 1938), or simply epithelioid modifications of the smooth muscle of the artery (Schumacher 1938).

Meijling (1938) claims to have observed a neurofibrillar network and Nissl's granules inside these cells. These observations could not be confirmed in the present specimens,and silver techniques, which have shown excellent neurofibrils inside the cells of the nodose ganglion, fail to reveal them in the epithelioid cells, which show only the characteristic argyrophilia. Meijling's diagrams are not at all convincing and Hollinshead (1943) has conclusively shown the inaccuracies of his observations.

Meijling/

Meijling seems to have mistaken the epithelioid cells for modified neurones. However, there are two points of interest in Meijling's paper. Firstly he finds no difference in the morphology of his modified neurones after nerve resection operations, just as is observed in the carotid body of the fowl, and secondly he describes the presence of his modified neurones as interlammelar groups of cells in the carotid sinus of the horse. Here his pictures are very suggestive of the argyrophil cells seen in the carotid body and carotid artery of the fowl.

The evidence seems to point to the fact that the carotid body of the fowl is an organ composed of a variety of tissues arranged in a definite manner. Its intimate relation to the vascular system is shown by the manner in which the whole organ lies in the course of its artery of supply, both being covered over by one continuous collagenous layer, which forms the adventitia of the artery and the capsule of the carotid body, while some of the cell elements (type II) lying entirely within the capsule appear to be derived from the muscle cells of the media. The absence of an internal elastic lamina in the artery of supply and within the blood spaces in the interior would appear to be an adaptation eminently suited to its function of recognising chemical/

chemical changes in the blood. The only aspect still undecided is the nature of the type I cells, which are peculiar to this organ and the related arteries. Their irregular shape (more marked in the wall of the carotid artery than in the carotid body itself) coupled with their strong argyrophil reaction suggest some similarity with other argyrophil cells in the body, namely the dendritic cells of the skin and the argentaffin cells of the gastrointestinal tract. Neural crest derivatives are notoriously hard to define and they may be as wide-spread as the peripheral nervous system itself. The morphology of the type I cells combined with their strict localisation to regions receiving a dense innervation makes it difficult to decide with certainty that they have no connection with the ectoderm.

It would seem, therefore, that from the structure and development of the carotid body in the fowl there is little doubt that this organ is the homologue of the carotid body of mammals. Whether or not its function is the same as that in mammals awaits clarification.

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REFERENCES

ADAMS, W. E. 1953. The carotid arch in lizards with particular reference to the origin of the internal carotid artery.
J.Morph. 92. 115-155.

ADDISON, W.H.F. and COMROE, J.H. (Jr.) 1937. The vascular relations of the glomus caroticum in the dog.
Anat. Rec. 67 (Suppl.). 2.

ASSENMACHER, D. 1953. Étude anatomique du système artériel cervico-céphalique chez l'Oiseau.
Arch. Anat.(Strasbourg). 35. 181-192.

DE BOISSEZON, P. 1936. La trifurcation carotidienne et le corpuscle intercarotidien du cheval.
Ann.Anat.path.méd.-chir. 13. 733-747.

———————1943. Les appareils de réglage de la circulation du corpuscle carotidien.
Bull.Histol.Tech.micr. 20. 136-150.

———————1944. Les vaisseaux, les nerfs. et les ganglions nerveaux dans la structure du corpuscle carotidien.
Bull.Histol.Tech.micr. 21. 54-64.

BOYD, J.D. 1937. The development of the human carotid body.
Contr.Embryol.Carneg.Instn. 26. 1-31.

DE CASTRO, F. 1928. Sur la structure et l'innervation du sinus carotidien.
Trav.Lab.Rech.biol., Univ.Madr. 25. 331-378.

CHOWDHARY, D.S. 1950. A note on the carotid body and carotid sinus of Varanus monitor.
Anat.Rec. 107. 235-241.

DUDLEY, J. 1942. The development of the ultimobranchial body of the fowl, Gallus domesticus.
Amer.J.Anat. 71. 65-97.

GOORMAGHTIGH, N. and PANNIER, R. 1939. Les paraganglions du coeur et des zones vaso-sensibles carotidienne et cardio-aortique chez le Chat adulte. Arch.Biol. Paris. 50. 455-533.

GOSSES, J. 1938. The Glomus caroticum. Acta.neerl.Morph. 1. 38-42.

HAMMAR, J.A. 1934. Konstitutionsanatomische Studien über die Neurotisierung des Menschen-embryos. I. Zur Bildungsgesegichte des Glomus caroticum. Z.mikr.-anat. Forsch. 35. 602-630.

HEWER, E.E. 1948. Text Book of Histology for Medical Students. 4th Edition. Heinemann. London. 173.

HOLLINSHEAD, W.H. 1941. A histological comparison of the carotid and coccygeal bodies. Anat. Rec. 79.(Suppl.2). 73.

———————— 1943. A cytological study of the carotid body of the cat. Amer.J.Anat. 73. 185-213.

HUGHES, A.F.W. 1934. On the development of the blood vessels in the head of the chick. Philos. Trans. B. 224. 75-129.

DE KOCK, L.L. 1951. Histology of the carotid body. Nature (Lond.) 167. 611-612.

KOHN, A. 1900. Ueber den Bau und die Entwicklung der sog. Carotisdrüse. Arch.mikr.Anat. 56. 81-148.

———— 1903. Die Paraganglien. Arch.mikr.Anat. 62. 203-365.

KOSE, W. 1902. Ueber das Vorkommen einer,, Carotisdrüse" und der,, Chromaffinen Zellen" bei Vögeln. Anat.Anz. 22. 162-170.

———— 1907. Die Paraganglien bei den Vögeln. Zweiter Teil. Arch.mikr.Anat. 69. 665-790.

MEIJLING, H.A. 1938. Bau und Innervation von Glomus caroticum und Sinus caroticus. Acta. neerl. Morph. 1. 193-288.

MURATORI, G. 1933. Ricerche istologiche sull'innervazione del glomo carotico.
Arch.ital.Anat.Embriol. 30. 573-602.

———————— 1934. Contributo istologico all'innervazione della zona arteriosa glomo-carotidea.
Arch.ital.Anat.Embriol. 33. 421-442.

NONIDEZ, J.F. 1935. The presence of depressor nerves in the aorta and carotid of birds.
Anat. Rec. 62. 47-73.

PAUNZ, L. 1923. Pathologisch-anatomische Veränderungen der carotisdrüse.
Virchows.Arch.path.Anat. 241. 76-115.

REIGELE, L. 1928. Die Nerven des Glomus caroticum beim Menschen mit kurzer Übersicht über den histologischen Aufbau des Organs.
Z.Anat. EntwGesch. 86. 142-167.

ROMANES, G.J. 1950. The staining of nerve fibres in paraffin sections with silver.
J.Anat.Lond. 84. 104-115.

SCHAPER, A. 1892. Beiträge zur Histologie der Glandula carotica.
Arch.mikr.Anat. 40. 287-320.

SCHUMACHER, S. 1938. Über die Bedeutung der arteriovenosen Anastomosen und der epithelioden Muskelzellen (Quellzellen).
Z.mikr.-anat.Forsch. 43. 107-130.

SMITH, C. 1924. The origin and development of the carotid body.
Amer.J.Anat. 34. 87-131.

SZEPSENWOHL, J. 1935. Le développement primitif de la glande carotidienne chez les embryons de canard.
C.R.Soc.Biol.(Paris). 119. 13-15.

TERNI, T. 1931. Il simpatico cervicale degli Amnioti.
Z.Anat.EntwGesch. 96. 289-426.

TWINING, G.H. 1906. The embryonic history of carotid arteries in the chick.
Anat.Anz. 29. 650-663.

UNGEWITTER, L.H. 1951. A urea silver nitrate method for nerve fibres and nerve endings.
Stain. Techn. 26. 73-76.

VERDUN, M.P. 1898. Sur les derives branchiaux du poulet.
C.R.Soc.Biol. (Paris). 5. 243-244.

WATZKA, M. 1934. Vom Paraganglion Caroticum.
Verhandl.Anat.Ges., Versamml. Wurzburg.
Anat.Anz. Erg.H. 78. 108-120.

WHITE, E.G. 1935. Die Struktur des Glomus caroticum, seine Pathologie und Physiologie und seine Beziehung zum Nervensystem.
Beitr. path. Anat. 96. 177-227.

DE WINIWARTER, H. 1939. Origine et developpement du ganglion carotidien.
Arch.Biol.(Paris). 50. 67-94.

ILLUSTRATIONS.

ABBREVIATIONS

Ac.d.n. : accessory depressor nerve.

Ar.c(s). : argyrophil cell(s).

art.cb. : artery to the carotid body.

art.ubb. : artery to the ultimobranchial body.

C. : capilarry spaces in the carotid body.

Cap. : capsule.

Car.a. and c.a. : carotid artery.

Car.r. : carotid ramus of the vagus.

c.a.s. : cervical air sac.

Cb. : carotid body.

Cb.an. : carotid body anlage.

epi.cs. : epithelioid cells.

Inf.thy.a. and I.T. : inferior thyroid artery.

Inf. pt. and I.Pt. : inferior parathyroid.

n.g. : nodose ganglion.

oe. : oesophagus.

Par. : parenchyma.

p.c. : precarotid trunk.

pc.c. : posterior strand of the precarotid trunk.

Pre.car.tr. : precarotid trunk.

Pc.gang. : precarotid ganglion.

Pt. : superior parathyroid.

S. : subclavian artery.

sec.sub. : secondary subclavian artery.

Ub.b. : ultimobranchial body.

Ub.b.art. : artery to the ultimobranchial body.

V. : vein.

V.A. : vertebral artery.

vas.sp. : vascular spaces.

Vg. : vagus.

I and II : epithelioid cells with vesicular and compact nuclei respectively.

III and IV : third and fourth aortic arches.